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THE MALE GAMETOPHYTE OF ABIES

A. H. HUTCHINSON

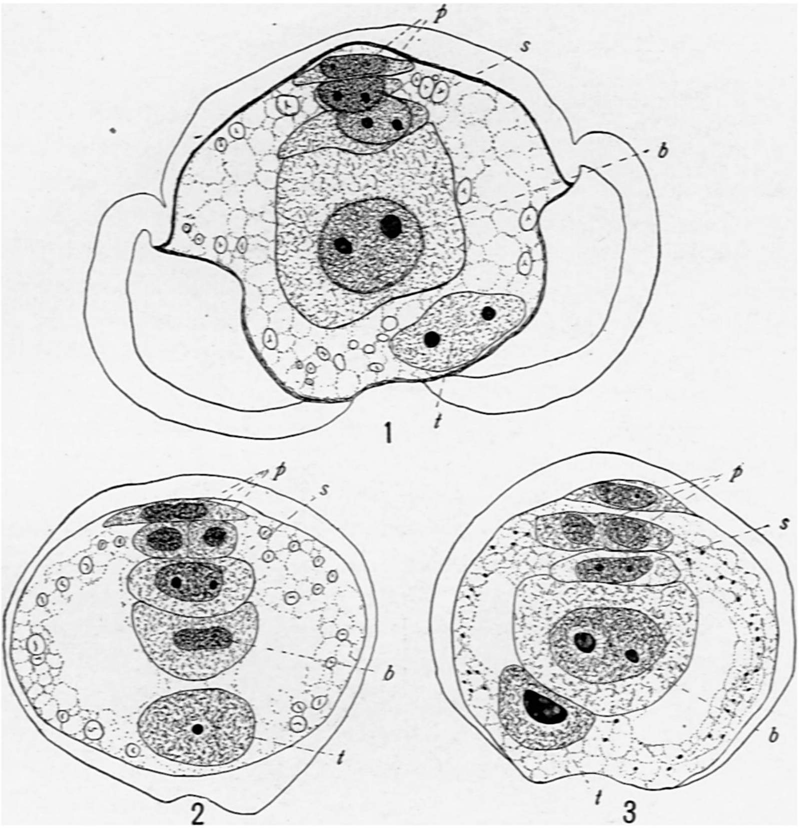
(WITH FIFTEEN FIGURES)

In a study of *Abies balsamea* as a type of the Coniferae, a number of irregularities in the contents of the pollen grain have been observed. Since the material used was collected from different trees and in different years, these irregularities cannot be regarded as abnormalities; and since further examination showed that similar conditions prevail in at least two other species of *Abies*, these observations have been thought worthy of record.

For the material I am indebted to Professor R. WILSON SMITH. *A. balsamea* was collected in Ontario; *A. Veitchii* and *A. brachyphylla* were obtained through the courtesy of the authorities of the Royal Gardens at Kew.

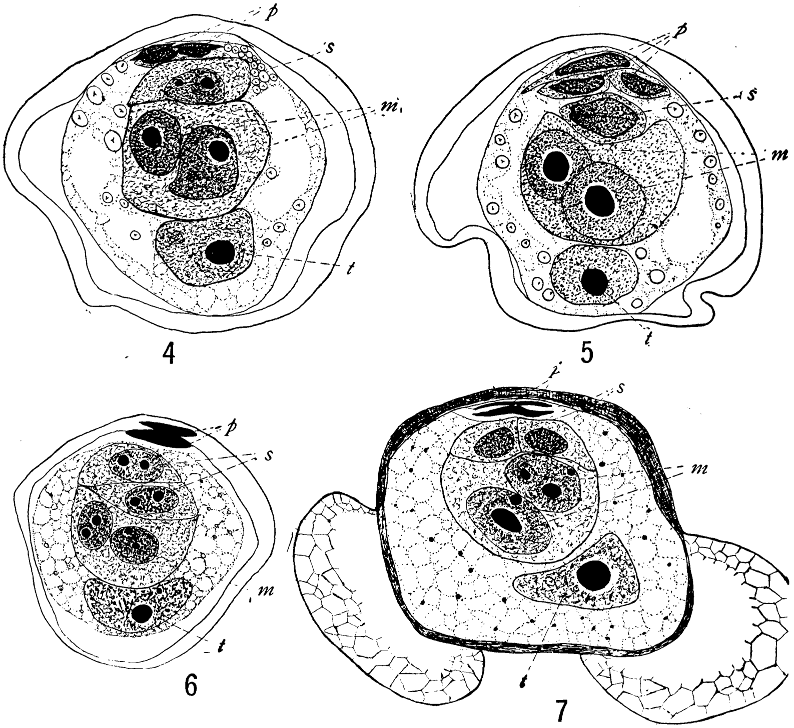
The pollen grain of *Abies balsamea* is very large, its diameter being about twice that of *Pinus*. At the time of shedding the normal grain contains two prothallial cells, a stalk cell, a body cell, and a tube nucleus, imbedded in a vacuolated protoplasmic mass which contains numerous starch grains (fig. 1). The nucleus of the body cell is surrounded by dense protoplasm and a cell membrane. The tube nucleus is large and usually compressed; in some instances the pressure, resulting from the extraordinary growth of the cells of the gametophyte, is insufficient to force it from its polar position to a lateral one. The stalk cell is much smaller than the body cell, and quite frequently is compressed into a cavity at the prothallial end of the latter. In *A. Veitchii* and *A. brachyphylla* the prothallial cells are very much flattened at this stage; but in *A. balsamea* it is not uncommon to find both prothallial cells retaining the characteristic nuclear structure. The size and permanence, however, varies with the individual as well as with the species.

The material examined does not show stages earlier than the division of the central cell into generative cell and tube nucleus. Peculiarities in this division are described later. The periclinal division into stalk and body cells takes place six or seven days before pollination. At this time the prothallial cells are at their maximum size.



FIGS. 1–3.—*Abies balsamea:* fig. 1, ripe pollen grain; figs. 2, 3, at time of shedding, showing divisions of prothallial cells; *p*, prothallial cells; *b*, body cell; *s*, stalk cell; *t*, tube nucleus; all ×610.

Frequent variations in the number of prothallial cells occur. The maximum number is four (figs. 2 and 4), but three are of more frequent occurrence (figs. 3 and 5). The division, as indicated by the position of the daughter cells, is anticlinal, either in or at right angles to the plane of the wings, hence they are best seen in a polar view. The presence of two derivatives of a prothallial cell, wher they lie one over the other, is easily overlooked. It is difficult, therefore, to determine the proportion of pollen grains in which there are more than two. In *A. balsamea* about 8 per cent show a division of one or both of the original prothallial cells; in *A. Veitchii* and *A. brachyphylla* the number is smaller. In some cases the separating wall, if formed, becomes obliterated and the appearance is that of nuclear division only (fig. 2).



FIGS. 4–7.—Figs. 4, 5, *A. balsamea* at time of shedding, showing divisions of prothallial cells and division of body nucleus into male nuclei (*m*); fig. 5 shows nuclear division in stalk cell; figs. 6, 7, *A. Veitchii*, showing two male nuclei, two derivatives of stalk cell, and prothallial cells much flattened; lettering as in the last; all ×610.

In approximately 10 per cent of the gametophytes the nucleus of the body cell divides before pollination into male nuclei. These are large and well developed, and imbedded in a common mass of protoplasm which is inclosed by the wall of the former body cell.

MIYAKE describes two male nuclei which enter the archegonium, and the one which fuses with the egg nucleus is said to be the larger. Before pollination, no difference in the size of structure could be detected (figs. 4 and 7), and MIYAKE's drawings show little or no difference in the pollen tube stage.

Occasionally the stalk cell also divides to form two derivative cells. The division is sometimes anticlinal (fig. 7), and sometimes periclinal (figs. 5 and 6). When this division takes place, the resulting nuclei frequently become uniformly granular and gradually degenerate. In this case also the separating walls are not always present (fig. 5) and the appearance is suggestive of amitosis.

There may be as many as four derivatives of the generative cell. In order to ascertain how many of the nuclei enter the egg at fertilization, an examination of the archegonium was made. Frequently there are four supernumerary nuclei at the micropylar end of archegonium after fertilization and during the proembryo stage (fig. 8). These in all probability are the second male nucleus, the two derivatives of the stalk cell, and the tube nucleus. MIYAKE states that these nuclei have the power of division. An examination of pollen grains lodged in the micropyle shows that while the other contents have passed into the pollen tube, the prothallial cells do not escape, but are retained by the intine in which they are imbedded.

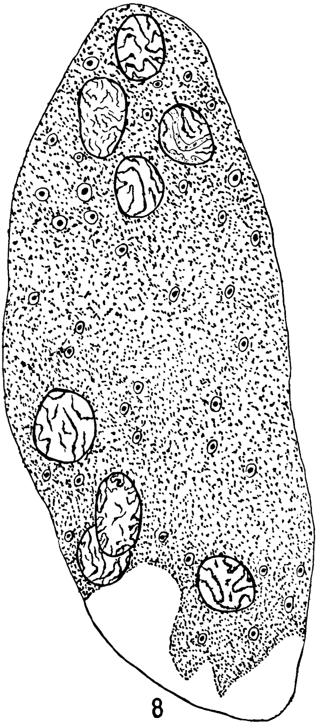
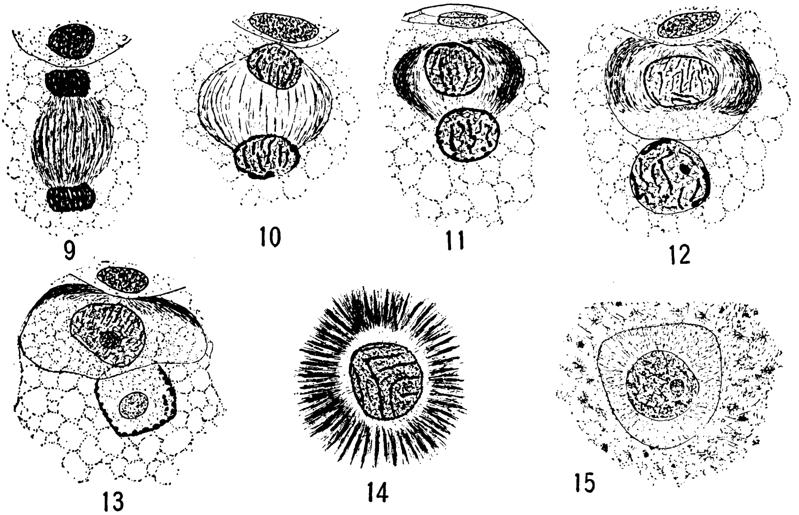


FIG. 8.—*A. balsamea:* embryo sac with four supernumerary nuclei at micropylar end, and first four nuclei of proembryo; ×610.

The division of the generative cell in *Abies* may be an adaptation to the rapid succession of events between pollination and fertilization: about 4 weeks in *A. balsamea* and 13 weeks in *Pinus*. *Picea* *excelsa* (POLLOCK) is similar in this respect. The division of the stalk cell cannot be so regarded; it may represent ancestral conditions. If so, it indicates a survival in *Abies* of a more ancient type of gametophyte than has been reported in any other of the Abietineae. Further, as the presence or absence of prothallial cells is a rather constant character of the different groups of Coniferae, and thus may have a phylogenetic significance, the presence of several prothallial cells may suggest a connection of the abietinean and araucarian lines; which connection is also indicated by evidence accumulating from other sources.



FIGS. 9–15.—*A. balsamea* ten days before shedding: figs. 9–13, successive stages in telophase of mitosis of central cell; the relative positions are indicated by that of the prothallial cell; fig. 14, polar view of stage shown in fig. 13; fig. 15, cross-section of generative cell below central line during stage shown in fig. 13, or just after formation of cell membrane; all ×926.

Certain peculiarities in the division of the central cell to form the generative cell and tube nucleus have been mentioned. Attention was drawn to these by the very conspicuous radiating strands which surround the generative nucleus, as seen in a polar view (fig. 14). Further investigation shows these to be derived from the spindle, and that they take part in the formation of the cell membrane.

In the late telophase no well defined cell plate is formed, although thickenings of the fibers may occur (fig. 9). The central fibers of the spindle disappear, either ceasing to be differentiated by the stain, or, as is more probable, they move out and become peripheral (fig. 10). Gradually the spindle widens and moves away from the tube nucleus, thereby inclosing the generative cell in the form of a hollow globe (figs. 10 and 11). The fibers continue to move upward until they come in contact with the wall of the second prothallial cell (figs. 12 and 13). Meanwhile the cell membrane is formed in the position occupied by the peripheral fibers. When the wall is complete the fibers have disappeared. Although derived from the spindle, the cell wall does not originate from a cell plate, but from the fibers after they have surrounded the generative nucleus. Whether or not the fibers fuse laterally is difficult to determine; that they are very numerous and form a dense, almost continuous, envelope about the generative nucleus is shown in a polar view (fig. 14). The definite cell membrane which is formed is best shown in cross-section. Fig. 15 represents such a section of a cell at the stage shown in fig. 13.

These peculiarities may perhaps be accounted for by the fact that the division is internal, and only one of the resulting nuclei is inclosed by a wall; hence this method of delimiting the cellular protoplasm. One is reminded of the formation of the plasma membrane about the ascospore of *Phyllactinia* as described by HARPER.

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